Voyage of the argonauts in the pelagic realm: physiological and behavioural ecology of the rare paper nautilus, *Argonauta nouryi*

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The metabolic demands of a rare paper nautilus, *Argonauta nouryi*, in the eastern tropical Pacific (ETP) are evaluated. After adjusting for temperature and size, the rates of oxygen consumption and of aerobic and anaerobic metabolic potential (as evidenced by citrate synthase and octopine dehydrogenase activities, respectively) of *A. nouryi* were much higher than those in holopelagic octopods that exhibit float-and-wait predation strategies. In fact, the rates were similar to those found in small epipelagic squids and benthic octopods. The critical oxygen partial pressure was 4.9 kPa at 20°C, suggesting that the strong oxygen minimum layer found at intermediate depths in the ETP may constrain the vertical distribution of *A. nouryi* to the upper few metres of the water column. We also report the occurrence of a chain of shelled females at the surface, in which each animal was attached, as if on the benthos, to the next individual in the chain. Although it may constitute an effective strategy to increase the rates of mate encounter in the vast open ocean, there may be an important ecological trade-off for such behaviour, namely the increase in visibility at the surface with concomitant attraction of predators.

Keywords: *Argonauta nouryi*, epipelagic ecology, hypoxia, metabolism, oxygen minimum layer, paper nautilus.

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Introduction

The paper nautilus, an octopod of the superfamily Argonautoida, is found worldwide in tropical and subtropical open oceans (Roper *et al*., 1984), but is rarely encountered. Reports of mass strandings (Norman, 2003) and their frequency in the stomachs of apex predators (Hernandez-Garcia, 2002; Pastorino and Tamini, 2002; Arizmendi-Rodriguez *et al*., 2006; Fonseca and Petry, 2007) suggest that they occur in large numbers, yet knowledge of their pelagic biology and ecology is surprisingly limited.

The most striking biological feature of the group is the acute sexual dimorphism. Females are much larger than males and secrete a delicate unchambered "shell", in which the eggs are brooded (Conrad, 1854; Naef, 1921–1923, 1977). The calcareous egg case is secreted and held by two modified dorsal arms with sail-like membranes, thought by their discoverers to be an aid to locomotion. Although similar in appearance, this fragile structure is totally distinct from the heavy multichambered shell of the true *Nautilus*. Males are substantially smaller, rarely more than 2 cm long, and, like other octopods, have a hectocotylized left arm III used for reproduction. The hectocotylized arm can be autotomized and left attached inside the mantle cavity of the female long after mating.

Argonauts also display unique behavioural and ecological adaptations to their oceanic habitat. For instance, they have been reported attached to, or in association with, gelatinous zooplankton (Table 1; Banas *et al*., 1982; Heeger *et al*., 1992; Norman, 2003). Females have also been observed attached to the shells of other argonauts in long chains, a curious behaviour described in more detail below. They are also capable of retaining gas bubbles inside the shell as a buoyancy mechanism (Boletzky, 1992). These behavioural adaptations may enhance energy saving by reducing the cost of transport and vertical support in the water column (Table 1). Nevertheless, some qualitative reports have indicated that argonauts are fast and muscular jet-propelled swimmers (Norman, 2003). Therefore, we would expect them to have high metabolic demands associated with the low propulsion (Froude) efficiency of jet swimming (O'Dor and Webber, 1986; Wells, 1990). Here, we evaluate, for the first time, the metabolic demands of *Argonauta nouryi*, captured at the surface of the eastern tropical Pacific (ETP). We also provide behavioural descriptions of the species, both in the wild and in captivity.

Material and methods

Female *A. nouryi* were collected in the ETP (8.59–8.55°N 90.00–85.50°W) aboard RV "Seward Johnson" (Harbor Branch) in November 2007 (Figure 1). In all, 18 animals were captured at the surface using a dipnet and immediately transferred into aquaria on board ship. They were maintained at 20°C for 4–10 h before being placed in a respiratory chamber. Just seven of them, ranging from 1.70 to 5.06 g total body mass, excluding shells (shell diameters varying from 19 to 25 mm), were in good physical condition and used in the physiological analyses.

Identification was based on the distinctive elongate shell (Figure 1a). *Argonauta nouryi*, also known as the long argonaut,

Table 1. Description of behavioural and ecological adaptations to the epipelagic ecosystem observed in argonauts.

Argonaut species	Number of individuals	Type of behaviour	Observations	Possible causal predictors	Source
Argonauta argo (greater argonaut)	1	Symbiotic association with gelatinous zooplankton	An argonaut was holding to the aboral surface of a scyphomedusa near the surface and feeding on its gastral cavity. The stinging capabilities of the cnidarian may also have provided protection, shelter, or camouflage against predators	F, P, C, T, and F	Heeger *et al.* (1992)
Unidentified species	2	Symbiotic association with gelatinous zooplankton	Two juvenile octopods were found in separate salp chains near the surface, inside an individual's pharyngeal basket	F, P, C, T, and F	Banas *et al.* (1982)
Argonauta hians (muddy argonaut)	1	Symbiotic association with gelatinous zooplankton	One octopod hanging on the aboral surface of a jellyfish near the surface and, presumably, capable of "manoeuvring" its host	F, P, C, T, and F	Norman (2003)
–	–	Gas retention	Although not demonstrated, it is thought that argonauts are capable of retaining external gas bubbles in the shell	F	Boletzky (1992)
Unidentified species (possibly *A. nouryi*)	–	Aggregation (possibly string formation)	In 1850, Capt. O. Swain of Nantucket observed a large number of argonauts (constituting just one group at first) that was moving quickly on the surface of the water, on a calm day	T and R	Conrad (1854)
Unidentified species	6	String formation	A moving rod was seen swimming beneath the surface at night. It rose quickly, swam along, and down out of sight. After approaching again, it was collected and identified as a string of six argonauts	T and R	Voss and Williamson (1971)
Argonauta nouryi (long argonaut)	18	String formation	A long, moving string of 18 argonauts, holding on to each other as a unit, was observed at the surface during a calm day in the ETP	T and R	Present study

F, food source; P, protection (shelter); C, camouflage; T, transport; F, flotation (buoyancy); R, reproduction (increased rate of mate encounter).

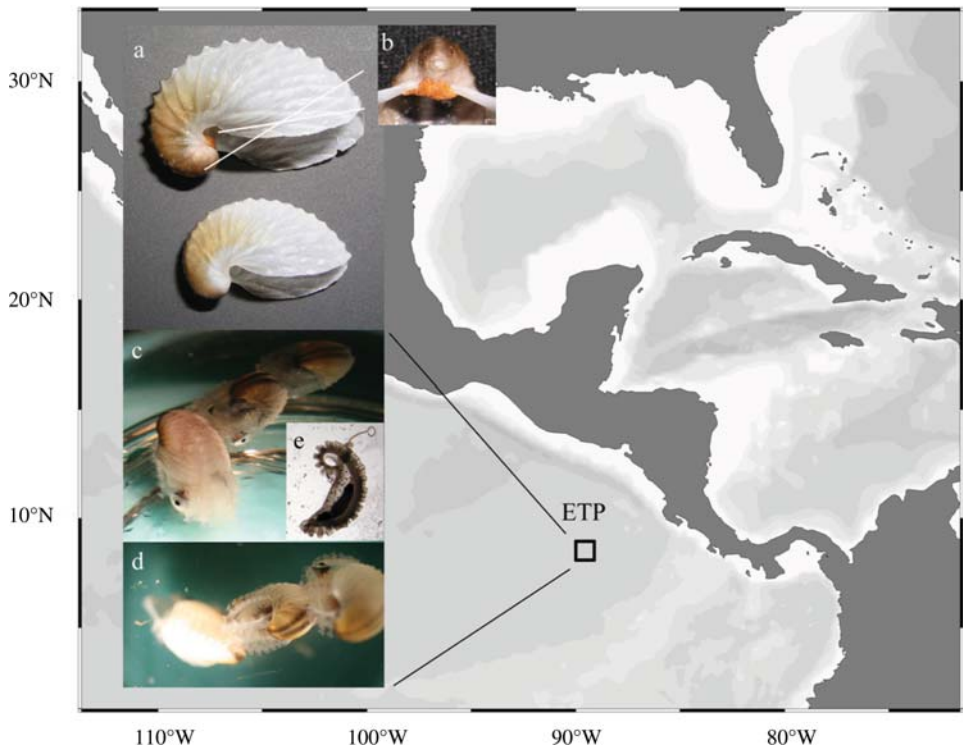

Figure 1. Sampling area (mark) in the ETP (8.59–8.55°N 90.00–85.50°W). (a) Shells of female *A. nouryi* (25 and 19 mm diameter); (b) view of brooding (orange) eggs; (c and d) side-oblique views of the smaller string-like formation of female *A. nouryi*, photographed in the shipboard aquarium; (e) microscopic view of a hectocotylus (the male reproductive arm, 2 mm long).

has a shell that is longer and smoother than those of other species, so is readily identified (Norman, 2003). The shells are white or cream in colour, with the oldest tubercles having a brownish pigmentation, and they possess many small knobs on the keel. The surface of the shell is smooth, and it has a large number of underdeveloped ribs.

Measurement of metabolic rate

Routine oxygen consumption rates were measured on board ship. Animals were placed in closed, water-jacketed respirometers (320 ml) containing 0.2 μm of filtered seawater with antibiotics (50 mg l^{-1} streptomycin) and allowed to deplete the available oxygen. Oxygen concentrations were recorded with Clarke-type O_2 electrodes connected to a Strathkelvin Instruments 928 Oxygen Interface. The system was calibrated using air- and nitrogen-saturated seawater and checked for electrode drift and microbial oxygen consumption before and after each trial. Temperature (20°C) was maintained with a recirculating water bath. The mean mass-specific rates of oxygen consumption (micromole O_2 consumed per gramme wet mass per hour), averaged between 30 and 70 mm Hg, were reported. The individual experiments lasted 1.5 h. Critical oxygen partial pressures (P_C; the point at which the rate of oxygen consumption is no longer maintained independent of oxygen partial pressure) were determined by plotting specific rates of oxygen consumption against oxygen partial pressure. Regressions were calculated for the two distinct sections of the curve, the regulated (higher PO_2) segment and the very sloped (low PO_2) segment. P_C was defined as the point where the two regressions intersected. After the respiratory experiments, the animals were weighed on a motion-compensated precision shipboard balance system (Childress and Mickel, 1980) and dissected. Mantle and arm tissues were frozen in liquid nitrogen and stored in the laboratory at −80°C until enzymatic analysis.

Measurements of enzymatic activity

Sections of ~0.1 g of mantle or arm tissue were homogenized in 0.01 mol l^{-1} Tris buffer (pH 7.5 at 10°C) in a dual hand-held glass homogenizer, kept on ice, and the homogenates were then centrifuged in an Eppendorf Centrifuge 5402 (Eppendorf, NY, USA) at 6600*g* for 10 min at 5°C. Samples (25 μl) of supernatant were placed in 1 ml quartz cuvettes under non-limiting substratum conditions, and the enzymatic activities were measured (at 20°C) using a Shimadzu UV160U spectrophotometer (Shimadzu Scientific Instruments, MD, USA) equipped with a water-jacketed cuvette holder connected to a recirculating water bath. The mitochondrial enzyme, citrate synthase (CS, E.C. 4.1.3.7), was assayed as an indicator of aerobic metabolic potential. The glycolytic enzymes, octopine dehydrogenase (ODH, E.C. 1.5.1.11) and lactate dehydrogenase (LDH, EC. 1.1.1.8), were assayed as indicators of anaerobic metabolic potential. The activities were expressed as units (micromole of substratum converted to product per minutes) per gramme of tissue wet mass.

Statistical analysis

Mass-specific metabolism and enzymatic activities (Y) typically change with increasing mass (M) according to the allometric equation $Y = aM^b$, where a is a taxon-specific normalization constant and b a scaling coefficient. Both oxygen consumption rates and enzymatic activities were evaluated in relation to wet mass, using the regressions in log-scaled plots. Regression slopes were declared significant when their slopes differed from zero at a 5% confidence level. Analysis of covariance (ANCOVA) was also used to compare differences in enzymatic activities of the different tissues analysed. The software Statistica version 6.0 was used.

Results

Routine metabolic rates and hypoxic threshold

Routine rates of oxygen consumption of *A. nouryi* varied between 1.7 and 5.1 μmol O_2 g^{-1} h^{-1} at 20°C (Figure 2) and, because of the small size range analysed, no significant relationship between mass-specific metabolism and body mass was observed ($p > 0.05$; Table 2). A mean critical oxygen partial pressure below which metabolism cannot be maintained independent of oxygen partial pressure, of 37 mm Hg was measured at 20°C (Figure 3). Based exclusively on the P_C (i.e. neglecting the species' anaerobic capabilities, see below), the vertical distribution of argonauts seems to be restricted to the epipelagic realm in the ETP.

Enzymatic activities

CS activities in the argonaut's mantle and arm tissues, an indicator of aerobic metabolic potential, are presented in Table 2. CS activities were significantly higher in the mantle than in the arms (ANCOVA, $p < 0.05$), ranging between 2.2 and 3.8 units g^{-1} and 1.3 and 2.4 units g^{-1}, respectively. However, the CS values were lower in the argonauts than in shallow-living benthic octopods (1.5–2 times lower in the mantle, and 1–1.2 times in the arms; Figure 4).

The anaerobic potential was determined based on the enzymatic activity levels of both ODH and LDH in mantle and arm tissues of the argonauts (Table 2). ODH activity ranged from 145.2 to 282.82 units g^{-1} in the mantle and between 38.05 and 74.70 units g^{-1} in the arms, significantly higher in the former tissue (ANCOVA, $p < 0.05$). After size normalization, mantle ODH activities were within the range previously reported for

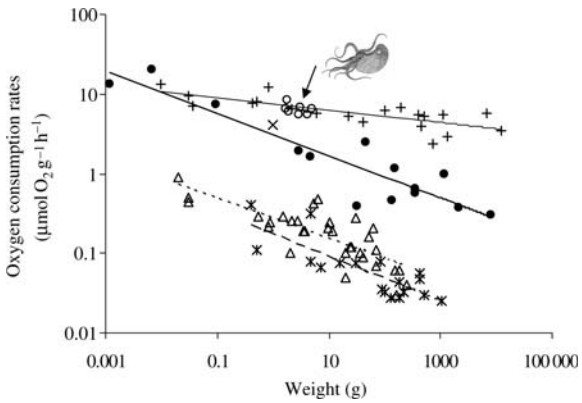

Figure 2. Mass-specific rates of oxygen consumption (μmol O_2 g^{-1} h^{-1}, at 5°C) of *A. nouryi* (open circles, normalized using a Q_{10} of 2.5) and other octopods, pelagic squids and vampire squid *Vampyroteuthis infernalis*, as a function of size. Open triangles, gelatinous pelagic octopods (*Japetella*, *Eledonella*, and *Amphitretus*); dots, muscular benthic octopods (e.g. *Octopus*, *Eledone*, *Paraeledone*, and *Bathypolypus*); crosses, the muscular pelagic octopod *Ocythoe tuberculata*; asterisks, vampire squid; plus signs, muscular pelagic squids (*Illex*, *Stenoteuthis*, and *Dosidicus*). The sources for the other cephalopod data are Seibel *et al.* (1997, 1998), Seibel and Childress (2000), Seibel (2007), and Rosa *et al.* (2009). The equation for the *A. nouryi* regression is given in Table 2.

Table 2. Mass-specific rates of oxygen consumption (μmol O_2 g^{-1} h^{-1} at 20°C) and CS, ODH, and LDH activities (units g^{-1} wet mass) in the mantle and arms of *A. nouryi* as a function of size.

			Tissues	
	Parameter	***Argonauta nouryi***	**Mantle**	**Arms**
Oxygen consumption ($MO_2 = aM^b$)	Mass (g)	1.70–5.06		
	Rate (μmol O_2 g^{-1} h^{-1})	22.05–32.60		
	a	29.54		
	b	−0.15		
	n	7		
	r^2	0.23		
Citrate synthase ($CS = aM^b$)	Mass (g)		1.97–5.06	1.97–5.06
	Activity (units g^{-1})		2.18–3.75	1.34–2.40
	a		4.28	2.61
	b		−0.24	−0.35
	n		5	5
	r^2		0.14	0.33
Octopine dehydrogenase ($ODH = aM^b$)	Mass (g)		1.97–5.06	1.97–5.06
	Activity (units g^{-1})		145.19–282.82	38.05–74.70
	a		137.2	39.85
	b		0.35	0.29
	n		5	5
	r^2		0.23	0.13
Lactate dehydrogenase ($LDH = aM^b$)	Mass (g)		1.97–5.06	1.97–5.06
	Activity (units g^{-1})		9.21–11.46	3.37–5.14
	a		12.35	3.23
	b		−0.18	0.20
	n		5	5
	r^2		0.60	0.13

In the allometric equation $Y = aM^b$, *a* is a taxon-specific normalization constant and *b* a scaling coefficient. *n*, number of specimens. For all variables, r^2 values were not significant ($p > 0.05$).

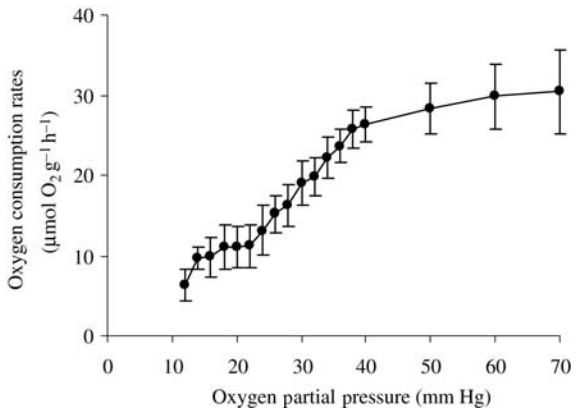

Figure 3. Mass-specific rates of oxygen consumption (μmol O_2 g^{-1} h^{-1}) averaged over 2-min intervals as a function of available oxygen (mm Hg) in *A. nouryi* at 20°C. Values represent the mean ± s.e. of the seven individual runs. Mean critical oxygen partial pressure (P_C) is 37.14 ± 6.20 mm Hg.

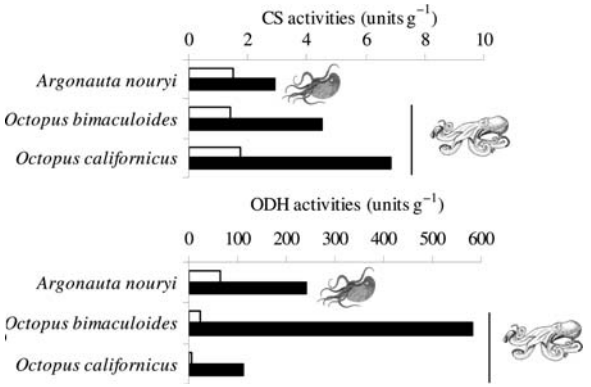

Figure 4. CS and ODH activities (units g wet $mass^{-1}$) in the mantle and arms of *A. nouryi* and shallow-living benthic octopods (normalized to 5 g wet mass). The source for the benthic data is Seibel and Childress (2000).

benthic octopods (Figure 4; Seibel and Childress, 2000). LDH activity was always less than ~10% of ODH and will not be discussed further (Table 2).

In situ and laboratory behavioural observations

Female *A. nouryi* were found drifting on the surface during the day. They were attached to each other forming a long chain of 18 animals. To our knowledge, this behaviour has been reported only twice before in unknown argonaut species (Table 1). After being collected and placed in the aquaria on board ship, most of them maintained this string-like formation. However, after a short time, the initial string started to separate into a few smaller formations of two or three females each (Figure 1c and d). Inside the respiration chambers, the argonauts tended to remain motionless, holding on to the walls with their suckers or lying on the bottom of the chamber. By the end of the

Table 3. Potential diet, prey caloric density, and daily foraging requirements (number of individuals) of *A. nouryi*.

Prey category	Prey caloric density (kcal g^{-1})	Foraging requirement* (*n*)
Copepods[a]	0.63[d]	50.41[f]
Hyperiid amphipods[a]	0.59[d]	53.66[f]
Pteropods[b]	0.66[d]	47.71[f]
Fish[c] (myctophids)	1.70[e]	1.86[g]

[a]According to Banas *et al.* (1982).
[b]According to Nesis (1977).
[c]According to Robson (1932).
[d]According to Davis *et al.* (1998).
[e]According to Childress and Nygaard (1973).
[f]Assuming a prey size of 0.01 g.
[g]Assuming a prey size of 0.1 g.
*To maintain a routine metabolic rate of 25.1 μmol O_2 g^{-1} h^{-1} (at 20°C, ~25 m) of a 5-g argonaut, assuming 4.7 kcal l O_2^{-1} and an assimilation efficiency of 100%.

experiments, all females had started to respond to hypoxia-induced stress by coming out of their brooding shells and sometimes ejecting ink. A male hectocotylus (still alive with flexing and curling movements) was found inside the respiration chamber after one female released itself from its shell (Figure 1e).

Discussion

Argonaut energy demand

Oxygen consumption rates (Figure 2) and metabolic potential (Figure 3) were high in argonauts, similar to the rates documented for epipelagic squids, which are among the fastest swimmers in the ocean (Figure 2). The fact that the activities of key metabolic enzymes are similar to, or lower than, those previously reported for both benthic octopods and epipelagic squids suggests that our metabolic rates are perhaps somewhat elevated by capture-induced stress and the relatively short incubation periods employed here. However, the rates we report for argonauts are clearly higher than those reported for deep-living holoplanktonic octopods (Seibel *et al.*, 1997). Interestingly, the metabolic rates of benthic octopods and epipelagic squids converge at a size of ~0.1 g (Figure 2). In other words, at that small size, the costs of constant swimming and predator avoidance in the well-lit surface ocean are negligible relative to other costs incurred by cephalopods (Seibel, 2007). It is therefore not surprising that many benthic octopods have pelagic juveniles (Boyle and Rodhouse, 2005) or that argonauts have adopted a holoplanktonic existence despite a tendency to use the bodies of gelatinous zooplankton as benthic substratum in the pelagic environment. It would be interesting to measure the metabolic rates of larger argonaut species to see if this habit results in rates that more closely resemble those of their more sluggish, benthic relatives than those of large active squids. The very low metabolic rates reported for gelatinous holoplanktonic octopods, even at small size, are explained by their deep-sea habitat. By reducing the predator–prey detection distance, low light levels below the photic zone dictate a locomotory habit and morphological adaptations that facilitate hypometabolism (Seibel *et al.*, 1997, 2000). For example, fin or medusoid swimming replaces inefficient high-speed jet propulsion at depth, whereas a gelatinous musculature reduces density and the cost of support in the water column, leading to a strong depth-related decline in metabolism. The rates of deep-sea octopods are lower than what can be explained by the effect of temperature and other abiotic and biotic factors, such as hydrostatic pressure, oxygen levels, and reduced food availability (Childress, 1995; Seibel and Drazen, 2007; Rosa *et al.*, 2008).

Argonauts feed on heteropods, pteropods (Nesis, 1977), small fish (Robson, 1932), and possibly hyperiid amphipods and copepods (Banas *et al.*, 1982). To meet the foraging requirements at 20°C (~25-m depth in the ETP), a 5-g argonaut has to consume the energy equivalent of ~2 small fish (myctophids, 0.1 g) or around 50 amphipods (0.01 g) per day to maintain its routine metabolic rate of 25.1 μmol O_2 g^{-1} h^{-1} (Table 3). Although our rates may be somewhat elevated over routine or field rates, the estimated requirement for food is conservative because additional food intake is required to promote growth and reproduction, and assimilation efficiency is never the 100% we have assumed for our calculations.

Hypoxia tolerance, vertical distribution, and the oxygen minimum layer

The high aerobic demands in *A. nouryi* suggest that its vertical distribution may be restricted to oceanic regions with high oxygen levels. However, in the ETP, this may include only the top few metres of the water column, because oxygen declines dramatically with depth (Karstensen *et al.*, 2008). The oxygen partial pressure at which an argonaut's rate of oxygen consumption is no longer maintained independent of the ambient oxygen levels is 4.9 kPa. This is much higher than the critical PO_2 for cephalopods known to migrate daily into the oxygen minimum layer [OML; jumbo squid, *Dosidicus gigas*, $P_C = 1.5$ kPa (10°C); Rosa and Seibel, 2008], suggesting that argonauts may be limited to the upper water column in the ETP. However, the metabolic rate and the critical oxygen level are sensitive to both temperature and stress and will decline with increasing depth. It is plausible that argonauts may overcome the high energy demands of their epipelagic existence by performing excursions to deeper and colder oceanic water. Moreover, metabolic suppression and high anaerobic potential, as indicated by high ODH activity, may constitute a viable physiological adaptation to survival in the OML (Rosa and Seibel, 2008, 2010). More-detailed physiological analyses are required to test these possibilities. At least under the present conditions (short incubations and high temperature), our observations of captive animals revealed that oxygen levels below the critical PO_2 caused apparent stress including, at the extreme, shell release.

Behavioural observations

The *A. nouryi* collected from the surface waters of the ETP were aggregated in a string of shelled females, in which one animal adhered to the shell of the subsequent individual in the chain. The reason for such behaviour is unclear. Female argonauts have been observed swimming "as a unit" within these formations before (Voss and Williamson, 1971), suggesting that swimming effort may be shared between individuals. The string can be separated into a few smaller formations of two or three females each (Figure 1c and d), as observed in nature before by Capt. O. Swain in 1850 along the coast of Peru (as described by Conrad, 1854). It was reported that "they appeared in large numbers, in one group at first, and then dispersed in smaller groups of twos and threes, moving with great rapidity over the surface".

Alternatively, increased conspicuousness of females in such a chain may increase the encounter rates and decrease the mating effort of males. In fact, finding mates represents a major challenge for pelagic animals (Buskey, 1998; Kiorbe, 2007). Rates of mate encounter will depend on the effectiveness of remote mate detection, which in turn may be enhanced by the unique swimming patterns of female argonauts in a chain. The most obvious explanation is that argonauts are effectively benthic animals that must spend most of their time attached to the substratum. The shells of their conspecifics provide such a base, as do a variety of gelatinous animals, in an environment where solid surfaces are otherwise absent (Gasca *et al*., 2007).

There is an important ecological trade-off for such female aggregations, however. Increased conspicuousness at the surface may attract potential predators. Based on historical descriptions (Conrad, 1854; Dall, 1869), surface aggregations may involve large numbers of individuals and, therefore, ultimately constitute an effective "fish aggregating device". In fact, structures that float on the surface of the ocean attract both juvenile and adult fish in great numbers and diversity (Castro *et al*., 2002). Aggregations of fish have been reported extensively around both man-made and natural drifting objects, such as logs (Greenblatt, 1979), jellyfish (Brodeur, 1998), and drifting algae (Kingsford, 1995). "Argonauts" are sometimes found in large numbers in the diets of some top predatory fish in the ETP (Rosas-Alayola *et al*., 2002; Arizmendi-Rodriguez *et al*., 2006), suggesting that they may be conspicuous targets.

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